# The jaguar's patches: viability of jaguar populations in fragmented landscapes

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## Abstract

Habitat loss and fragmentation have serious consequences for long-term population persistence, thus we investigated the effects of these processes on jaguars (*Panthera onca*) across the species' distribution range. We employed theoretical simulations of population dynamics, making use of real and hypothetical landscapes to understand how landscape patterning affects the long-term persistence of species, and investigated the isolated and synergistic effects of habitat loss and fragmentation. Jaguar persistence probability was related both to the amount and pattern of landscape subdivision, but with a strong tolerance for habitat loss because the amount habitat could be between 230 to 5841 $km^2$. In contrast, the persistence probability of smaller jaguar populations decreased dramatically in fragmented landscapes, indicating that fragmentation is a greater threat to jaguar long-term viability than habitat loss. Only two of the 28 populations included in our study were deemed viable in the long-term. Given the increase in habitat fragmentation and the current threat status of the jaguar, we discuss the best strategies for their conservation.



## Keywords

Critical threshold, habitat loss, habitat fragmentation, *Panthera onca*, population viability analyses

## Introduction

Human land use and habitat conversion are a central topic in conservation biology because they are largely responsible for the current and alarming biodiversity extinction rate (Foley et al., 2005). The conversion of native vegetation into anthropogenic cover alters landscapes, fragmenting habitats while simultaneously reducing their extent (Fahrig, 2003). Thus, habitat loss and fragmentation are simultaneous processes arising from human-induced landscape changes (Andrén, 1994; Fahrig, 2003). Nevertheless, habitat loss and fragmentation can be considered different processes, since habitat loss infers a decrease in available habitat while fragmentation refers to habitat subdivision into smaller patches (Andrén, 1994; Fahrig, 2003). Despite inherent difficulties, it is critical to understand the differing effects of each process in order to better guide wildlife management strategies, permitting a more efficient use of limited conservation resources (Lindenmayer & Fischer, 2007; Smith et al. 2009). Therefore, to generate a broad picture of the consequences of habitat loss and fragmentation, studies should understand the synergistic effects of both process, as well as their isolated effects.

Landscape metrics provide an excellent tool to enable the study of synergistic and isolated effects of habitat loss and fragmentation (McGarigal & Cushman, 2002). Currently, hundreds of metrics have been described and these are frequently used to capture landscape patterns resulting from complex interactions between habitat loss and fragmentation in real landscapes (McGarigal & Marks, 1994). However, they are also able to represent simple patterns. Habitat area reductions in time or space are a measure of habitat loss (Fahrig, 2003), and the total habitat or proportion of habitat in a landscape can represent this process. Similarly, the number of patches and their relative size are metrics commonly used to quantify fragmentation (Fahrig, 2003). Thus, total habitat area and the number of patches are a good representation of the isolated effects of these processes.

59 Even with the development of landscape metrics, it is difficult make general
60 predictions about the effects of habitat conversion because it may be perceived different by
61 species (Lindenmayer & Fischer, 2007), so a species-specific approach is essential to measure
62 the effects of habitat loss and fragmentation. Population viability analysis (PVA) has become
63 a useful tool because it facilitates the evaluation of individual species' responses to a variety
64 of environmental threat scenarios, generating an estimate of persistence probability (Brook et
65 al., 2002). Therefore, the combination of PVA and landscape metrics should be an efficient
66 approach to investigate individual species' responses to landscape patterns.
67 The goal of our study was to investigate the synergistic and isolated effects of habitat
68 loss and fragmentation to understand how landscape patterning affects the long-term
69 persistence of species. For this, we selected the jaguar (*Panthera onca*, Linnaeus 1758) as a
70 focal species, because jaguars occupy less than 60% of their former geographic range
71 (Morrison et al, 2007). The jaguar is ranked 15$^{th}$ among the large-bodied mammals with the
72 greatest geographic range contraction in the last 500 years due to anthropogenic effects
73 (Morrison et al., 2007). Today, the jaguar is listed as Near Threatened (IUCN, 2013), but this
74 status may soon be revised to reflect further declining populations (IUCN, 2013).
75 To achieve our objectives, we first investigated the synergistic effect of habitat loss
76 and fragmentation. The present-day habitat configuration can be considered as a pattern
77 generated by the effects of both processes because it is a result of past habitat loss and
78 fragmentation (Villard & Metzger, 2013). Therefore, we used real landscapes where the
79 species is present to investigate how the landscape configuration could determine jaguar
80 persistence probability. To better understand the consequences of habitat configuration on
81 species persistence, we created hypothetical landscapes based on the simplest landscape
82 features, i.e. the total habitat area and the number of patches. For that, we modeled jaguar
83 population dynamics in landscape scenarios for (i) a controlled number of patches while

reducing the total habitat area, and (ii) a controlled total habitat area while increasing the number of patches. The generation of the hypothetical landscapes mirrored the processes that produce real landscapes, which allowed us to better comprehend habitat configurations, but also allowed us to disentangle the effects of habitat loss and fragmentation on populations and to determine which effect is the greatest threat to jaguars.

Each step of our study resulted in an applied outcome, which can inform jaguar conservation and management strategies. The evaluation of jaguar population dynamics in real landscapes permitted us to map threatened populations and to highlight those that need urgent intervention to persist in the long-term. The hypothetical landscapes helped us to identify the amount of habitat necessary to maintain viable populations and the extent of habitat fragmentation a jaguar population can support while maintaining a high persistence probability. Thus, they helped in determining the best management strategies, and provided general insight into the importance of increasing total habitat area and connecting isolated fragments to ensure the long-term persistence of jaguar populations across its range.

## Methods

### *Study Area*

To conduct our investigation, we selected jaguar populations where density estimates were available. We used the review of Maffei et al. (2011) as our primary source for study areas, where authors reported jaguar densities for 49 study areas distributed across 14 countries. However, the studies considered in that review used different density estimation methods and sampling designs, so we selected sites where densities were estimated by the same method to ensure consistency, capture-recapture using two camera-traps at each sampling station as the census technique. Among the evaluated studies, 28 fulfilled the

prerequisites and were selected for our investigation. These studies correspond to areas located throughout nine countries, with density estimations varying from 1.12 to 11.56 jaguars/100 $km^2$ (Supplementary Material A).

*Landscape scenarios*

The real landscapes were delimited by establishing a 10,000 $km^2$ buffer around the central point where the density studies were conducted. We used the GlobCover map (ESA, 2011) to define the land use across landscapes, and converted GlobCover classification into a binary map to approximate a jaguar's perception of the landscape: we categorized native vegetation cover as suitable for jaguars and anthropogenic landcover as unsuitable. This level of generalization was adopted because jaguars show significant environmental plasticity in terms of their use of vegetation types (Colchero et al., 2011), and although it is known that jaguars occupy anthropogenic vegetation (Colchero et al., 2011), it may be that they simply traverse these areas rather than occupy them. Additionally, jaguar mortality probably increases in anthropogenic vegetation (Inskip & Zimmermann, 2009), justifying our classification of it as unsuitable for jaguars. The number and size of habitat patches were estimated for each landscape in the jaguar habitat map. Patches larger than 100 $km^2$ were included in our PVA because we considered that these patches adequately function as stepping stones and since it is a reasonable size for a jaguar home range (Cavalcanti & Gese, 2010; Cullen Jr., 2006).

The hypothetical landscapes were designed with a controlled structure to measure the effects of habitat area and subdivision. The simulations started considering a landscape with the maximum of structural integrity, i.e. a patch of 10,000 $km^2$. In order to model the effects of habitat loss, the total area was reduced gradually, by blocks of 1,000 $km^2$, until only 1,000 $km^2$ remained, and then to 500 $km^2$ and finally to 100 $km^2$. In order to model the effects of

habitat fragmentation, the total area of habitat was kept constant (i.e. the same amount of habitat used in the habitat loss simulations), but it was divided into a number of scenarios where we gradually increased the number of patches. The first scenario had two patches, the second had four patches of equal size, continuing progressively by steps of four up to 28 patches. The patches were of equal area without reducing the total area, and so each patch had equivalent relevance to population persistence.

*Population Viability Analysis*

The software VORTEX version 9.99 (Lacy, 2012) was used to simulate the population dynamics of jaguars and estimate persistence probability for 200 years. VORTEX is a Monte Carlo simulation that considers a set of factors affecting a population, including: deterministic forces (e.g. trends in carrying capacity); demographic, environmental and genetic stochasticity; and catastrophes (Lacy, 2000). We chose VORTEX due to its spatially-implicit approach, which was necessary for our study because the literature concerning the jaguar lacks information about dispersal rates and mortality in different landcover types and areas.

Most of the life history data were obtained from the 'Brazilian Action Plan for Jaguars' because it compiles the most up-to-date biological data on the species (de Paula et al., 2010) (Table 1). These data represent an actual, but non-specified, jaguar population (de Paula et al., 2010), so the population might be derived from anywhere within the species distribution. We used the same life history data to all populations modeled in our study, thus the differences among populations regarded landscapes proprieties where they are located. Due to the spatially-implicit approach, the total habitat area and the number of patches were integrated into the PVA indirectly; the number of patches was used as a surrogate for the number of populations and the total amount of suitable habitat was a surrogate for population

size. The total area of the patches multiplied by the jaguar density determined initial population size.

We assumed that carrying capacity was equal to the initial population size, which was a conservative approach because there is no information about the temporal change in carrying capacities of these studies areas. There is also no information about jaguar dispersal rates or mortality in the different landcover types. Therefore, we chose a generalized approach, whereby the movement of migrants between fragments was considered symmetric, i.e. individuals could move in either direction between patches at the same rate. The total number of migrants was estimated as a function of the number of subadults in the population because, typically, at this life-history stage, felines are looking to establish a territory (Funston et al., 2003). The proportion of subadults was determined as a proportion of the dynamic sites (*sensu* Gotelli, 1991) that can be occupied in the metapopulation. Since a subadult competitively excludes another individual from its *site*, the excluded jaguar (which can be an adult or another subadult) can compete for another *site* in the metapopulation. Therefore, the number of subadults defined the proportion of dispersers, but the dispersers could be any jaguar in the population.

Of the estimated life-history parameters for jaguars, the percentage of males in the breeding pool and mortality were those having the greatest degree of uncertainty. The percentage of males in the breeding pool is difficult to estimate. An accurate estimate would require long-term demographic study, using expensive techniques, such as genetic analysis and GPS monitoring. Mortality too is a complex parameter that varies according to sex, age and location (Ferreras et al., 2004), as well as anthropogenic factors (Inskip & Zimmermann, 2009). We modeled PVAs based on the best preserved landscape in our study area (jaguar density of 11.56 jaguars/100 $km^2$ and 10,000 $km^2$ of available habitat; Miller & Miller unpublished data; to review, see Maffei et al. 2011), with different values for the percentage

of males in the breeding pool and jaguar mortality to take into account the uncertainty of these parameters. The proportions of males in the breeding pool used in the models were 100%, 80% and 70% while, for mortality rates, we used 10%, 30% and 50% (for both sexes and every age class). These values were attributed randomly into the 500 PVA models.

*Statistical Analysis*

To investigate the synergistic effects of habitat loss and fragmentation on jaguar population viability, we used landscape metrics as a measure of landscape configuration. We calculated landscape metrics using the Fragstats software program (McGarigal & Marks, 1994) on a landcover map (Bontemps et al., 2011), with our classification of suitable/unsuitable habitat for jaguars. The selected metrics included: the proportion of native cover in the landscape (PLand); largest patch index (LPI); landscape shape index (LSI); patch number (PN); cohesion; mean size of patches (Area-MN); and the standard deviation of patch area (Area-SD) (Table2). These various landscape metrics might capture the same process, resulting in over-parameterization of the statistical analysis. Thus, we conducted a principal components analysis (PCA) to remove redundant parameters (Legendre & Legendre, 1998), and the associated principal component scores were used to represent the landscape configuration.

The real landscapes studied could be spatially structured throughout the jaguars' distribution and may depict spatial autocorrelation, so we adopted the use of spatial filters as a covariable to address this problem. Spatial filters consist of synthetic variables added into analyses with the objective of expressing the geographic relationships among landscapes (Dray, 2011; Patuelli et al, 2010). They capture orthogonal variation in spatial structure at different scales without inserting redundant parameters (Diniz-Filho & Bini, 2005). Spatial

208 filters are eigenvectors from a principal coordinates analysis of neighbor matrices (Borcard &
209 Legendre, 2002), calculated through the truncated distance matrix *W*

$$W = (w_{ij}) = \begin{cases} 0 \rightarrow i = j \\ 0 \rightarrow d_{ij} > t \\ \left[1 - (d_{ij} / 4t)^2\right] \rightarrow d_{ij} \leq t \end{cases}$$

210

211 where *wij* is each one of the elements and *t* is the truncation distance. The spatial filters were
212 generated by the Spatial Analysis Macroecology software (SAM) (Rangel et al., 2010) based
213 on the geographical distance between landscape centroids.

214 Model selection was performed to evaluate the best model explaining the relationship
215 between persistence probability, landscape configuration and spatial filters. This was
216 accomplished through the use of the Akaike Information Criterion corrected for small sample
217 size (AICc) (Burnham & Anderson, 2004), which permits a hierarchical ordination of models
218 according to their descriptive power and complexity (Burnham & Anderson, 2004). We
219 expected to generate a non-linear pattern of species responses to habitat loss and
220 fragmentation (Swift & Hannon, 2010), so we used a logistic adjustment for our models to be
221 more consistent with theory. We also included a model composed only of a linear coefficient
222 to evaluate if a random solution explained the persistence probability better than the proposed
223 variables. We considered models with AICc values lower than two as complementary
224 explanations of pattern (Burnham & Anderson, 2004), since the null model was not among
225 the best solutions.

226 To measure the amount of habitat necessary to maintain a viable population of
227 jaguars, and the extent of fragmentation a jaguar population can support while maintaining its
228 viability, we performed a piecewise linear regression with the hypothetical landscape data.
229 Piecewise analysis estimates the tipping point at which system alteration generates qualitative
230 changes in population persistence probability, i.e. from viable to nonviable. This tipping point
231 is known as the critical threshold and it is defined as an abrupt and non-linear alteration in a

given variable occasioned by small changes in the original system (Fahrig, 2001; Scheffer et al., 2009). Mathematically, piecewise analysis adjusts more than one regression line through data variation, and the "breakpoint" (or the place where the lines converge) is considered the critical threshold (Toms & Lesperance, 2003). We calculated the critical threshold using the *SiZer* package (Sonderegger, 2011) in R software (R Core Team, 2013).

The sensitivity of our base population viability model was investigated using a regression tree (Cutler et al., 2007; Harper et al., 2011), which permits the evaluation of multiple uncertain parameters and their nonlinear interaction (Harper et al., 2011). The regression tree structures data through hierarchical and binary partitions (splits) to create groups (nodes) of higher homogeneity, reflecting parameter importance, up to an undivided group of populations (leaves) (Rejwan et al., 1999). The evaluation of node numbers in the regression tree was accomplished by a cross-validation procedure, which calculates the true prediction error in the addition of nodes (Breiman, 2001). A random forest was performed to evaluate the relative importance of each parameter in the PVA estimations (Cutler et al., 2007), which indicated the variable that needed to be more accurately estimated (Harper et al., 2011). The random forest analysis was carried out using 1000 random trees through bootstrap sampling (Breiman, 2001). We used the *rpart* (Therneau et al., 2011) and *randomForest* (Liaw & Wiener, 2002) packages to conduct the regression tree and random forest analyses in R software (R Core Team, 2013).

**Results**

The studies areas had a large proportion of suitable habitat (Average PLand = 77.7%), which could be divided from one to five patches larger than 100 $km^2$ (Supplementary material A). However, we observed that the landscapes composed of habitat aggregated into one single patch had a larger proportion of suitable habitat than landscapes with two or more

patches ($\overline{X}$ $PLand_{2\text{-}5patches}$=65%; $\overline{X}$ $PLand_{1patch}$=87%; t-value = 2.18; DF = 26; p = 0.04). Even same with this difference, the landscape metrics used to calculate the configurations of real landscapes were correlated. Therefore, we selected only the first principal component of the PCA according to a broke-stick method, which described 58% of the landscape metrics variation. The variables PLand, LPI, Area-MN, Area-SD and cohesion were positively correlated with the principal component, while PN and LSI were negatively correlated.

Two out of the 64 competitive models were considered the best (i.e. AICc < 2) in explaining the persistence probability of jaguars in the landscapes, the null model not being amongst them (Table 3 and Supplementary Material B). The principal component condensing the landscape configuration appeared in both models (Table 3), evidencing the homogenous effect of landscape configuration, which could be observed due to the low variance in the coefficient value and the low standard error of the competitive models (Figure 1). Spatial filters three and five also appeared in the best models, but had large standard errors associated with them, obscuring their importance in predicting persistence probability (Table 3). Therefore, we considered only the principal component summarizing landscape configuration as an efficient predictor of jaguar persistence probability.

The habitat loss critical thresholds varied widely among jaguar populations, attaining values ranging from 230 $km^2$ to 5,841 $km^2$ (Figure 2 B). These values were strongly correlated with jaguar density (Figure 3 A) due to the direct effects of initial population size on persistence probability. Variation in the order of decimal degrees generated changes of more than 100 $km^2$ in the critical threshold. However, the fragmentation critical threshold was more sensitive to changes in the landscape than the habitat loss critical threshold. The tolerance of jaguar populations to fragmentation was not sufficient to determine fragmentation critical thresholds; the piecewise linear regression calculated the critical thresholds when the metapopulation had a persistence probability close to zero (tipping points have a negative

slope). In only a few cases did the populations have a high persistence probability after the first subdivision, even in landscapes with 10,000 $km^2$ of suitable habitat (Figure 4).

As a complementary result, we calculated a habitat critical threshold with a 97.5% confidence interval, to have a conservative estimate of ensuring long-term jaguar persistence. When populations had a density greater than 4.13 jaguars/100 $km^2$, jaguar population viability suffered an abrupt and stable change following a small reduction of habitat, which resulted in almost uniform residuals and an inadequate fit of the piecewise-regression to bootstrap samples. This mathematical artifact generated a relationship between density and the critical threshold similar to a parabola, in which the estimated density decreases to 4.13 jaguars/100 $km^2$ and thereafter starts to increase (Figure 3 B). Of course, there is no biological sense to this pattern since the area needed to maintain a jaguar population must decrease with higher density. Thus we considered it acceptable, from a conservation perspective, to consider the threshold estimated at 4.13 jaguars/100 $km^2$ for populations with greater densities. Based on that, the jaguar habitat critical threshold with a 97.5% varied from 3,000 $km^2$ to 7,000 $km^2$ (Supplementary Material A).

The real landscapes evaluated were able to support a jaguar population only in two out of the 28 sites investigated (Figure 2 B; Supplementary Material A), based on 95% persistence probability after 200 years (Table 1). Both of these viable populations are located in Guatemala and exhibit high jaguar density and a landscape with almost 100% native vegetation. Many other high density populations were nonviable (Figure 2 B and Supplementary Material A). These landscapes frequently had a total area that was larger than the habitat loss critical threshold, but the area was divided into a number of patches that were also larger than the fragmentation critical threshold, which resulted in nonviable populations. Therefore, the main threat to the long-term persistence of the jaguar populations studied seemed to be habitat fragmentation.

The sensitivity analysis showed that 82% of the predictors' variance could be explained by random forest. The regression tree was composed of six nodes, all defined by female mortality (Figure 5). Therefore, the PVA model was sensitive to poorly-estimated parameters, especially adult female mortality (Figure 6). The final node showed the populations with higher persistence probability, which were those with a female mortality rate lower than 20% from birth to sexual maturity (i.e. three years of age) (Figure 5). Thus, low mortality in female jaguars may be seen as a surrogate of population persistence probability.

## Discussion

Jaguar persistence probability is linked to landscape configuration in an ecologically complex and interesting way. The proportion of suitable habitat in the real landscapes predicted jaguar persistence probabilities - it being greater when the habitat is aggregated in one single patch, which was reinforced by the simulations on hypothetical landscapes. However, although we have shown that a high proportion of habitat could guarantee long-term jaguar persistence, we have also shown that habitat subdivision dramatically reduces their persistence probability, even in landscapes with a large proportion of suitable habitat and a high jaguar density. Therefore, we can confirm that fragmentation is more detrimental than habitat loss to jaguar populations.

The correlation among metrics of the real landscapes is a product of the large amount of suitable jaguar habitat. Landscapes comprising an amount of suitable habitat greater than 65% are structurally connected and display low structural complexity (Bascompte & Solé, 1996; With, 1997), which is the case for the majority of our study areas. Therefore, habitat loss and fragmentation are processes that can homogenize landscape configurations. Based on that, we could also expect that the landscapes composed of habitat aggregated into one single patch had tended to have a larger proportion of suitable habitat than landscapes comprised of

two or more patches, and this was supported by the real landscapes analyzed in the current study. Therefore, the relationship we found between total habitat availability and persistence probability expresses more than a simple metric for the predictability of an ecological process. The increase in availability of suitable habitat acts directly on landscape connectivity, thereby altering population structure (Bascompte & Solé, 1996).

The low persistence probability of jaguar populations in fragmented landscapes is probably linked to an increase in overall mortality, arising by impediments to dispersal. We established a stable proportion of migrants and survivors between patches in our models, so total mortality increased with an increase in the number of patches. The effects of mortality were reinforced by our sensitivity analysis, especially for female mortality, since the PVA estimates were sensitive to this parameter. Jaguar mortality can vary widely among populations because it is strongly influenced by extrinsic factors (Azevedo, 2008; Polisar et al., 2003). However, it seems reasonable that female mortality at the reproductive stage is important because a relationship between the total number of females in the reproductive pool and growth rate is expected for a polygenic species. Even though this parameter is quite relevant for jaguar ecological studies, there is no information about the variability and intensity of jaguar mortality in terms of sex, age or matrix type. This resulted in persistence probabilities that were sensitive to poorly-estimated parameters. However, an increase in mortality during dispersal in a fragmented landscape can be expected, as we assumed in our models even with the different rates we used. Thus, while our results might vary in intensity with better model paramaterization, the overall findings would not change.

*Conservation implications*

Our approach permitted us not only to summarize the effects of habitat loss and fragmentation on jaguar persistence probability, but also to generate a diagnostic of jaguar

conservation status because all the results discussed here have strong applicability from a conservation perspective. According to our results, we can predict that jaguar conservation is in a dangerous situation, given that only two of the 28 evaluated populations had a high probability of persistence. Over recent years, the species has become more dependent on protected areas (Riley, 2006), but currently few such areas can support demographically-viable jaguar populations (Sollmann et al., 2008). Thus, our results provide an important contribution to jaguar conservation because the habitat loss critical thresholds can be used to predict the necessary size of protected areas (Traill et al., 2007; 2010).

Even with our growing dependence on protected areas for species conservation, many are not fulfilling their conservation function because they do not support long-term viable populations (Sollmann et al., 2008). We can highlight Iguaçu National Park (INP) and its surrounding areas as a significant example because it supports one of the few remaining southern jaguar populations located in an area with large suitable habitat fragments (Altrichter et al., 2006; Mazzolli, 2009). However, the jaguar population in this landscape is highly vulnerable to extinction (Persistence Probability < 0.01, Mean time to extinction = 58.7 years), even though the landscape comprises 9,200 $km^2$ of native vegetation cover in a practically single and large patch. The unviability of this population might be due to the low number of individuals it harbors, since it had the lowest density of all the locations evaluated in this study. Due to the time lag of species' responses to environmental alterations, especially those species of significant longevity (Krauss et al., 2010) such as jaguars, the mean time to extinction can be higher than those estimated. Nevertheless, INP still has one of the most threatened jaguar populations. The areas surrounding INP suffer from severe hunting pressures (Azevedo, 2008), which decrease jaguar population density both directly by poaching and indirectly by prey reduction.

Currently, the implementation of dispersal corridors is the main strategy recommended by researchers and conservation managers to bolster threatened jaguar populations and to connect protected areas (e.g. Rabinowitz & Zeller, 2010; Rodríguez-Soto et al., 2013). Our study provides theoretical evidence for low jaguar persistence probabilities under metapopulation dynamics (Figure 4). Thus, the establishment of dispersal corridors needs to be carefully planned, given that the negative consequences of fragmented metapopulation dynamics could be worse than those for populations that remain isolated (Brito & Fernandez, 2002). A corridor can force species to cross less-suitable habitats (Franklin & Lindenmayer, 2009). For top-predators such as jaguars, this can exacerbate retaliatory hunting in response to the intensification of jaguar predation on domestic animals (Inskip & Zimmermann, 2009), which would probably occur in these contexts.

Therefore, our results raise the question of how to manage jaguar populations in fragmented landscapes. Perhaps jaguar conservation planning should emphasize strategies that increase population size by decreasing human-wildlife conflicts and increasing habitat quality. Decreasing human-wildlife conflict will depend on multiple factors because it has an ecological, social and probable regional context (Zanin et al. unpublished data). Increasing habitat quality is also a complex task because it will involve landscape management - though the field of restoration ecology is rapidly advancing, which will be of assistance in this area. Our research highlights the fact that jaguar conservation is far more complex than the connectivity between two areas, as has been suggested by researchers (Rabinowitz & Zeller, 2010; Rodríguez-Soto et al., 2013). Of course, the implementation of dispersion corridors is of fundamental significance for long-term jaguar conservation in some regions, but its applicability should be evaluated carefully and in conjunction with efforts to maintain or grow local jaguar populations.

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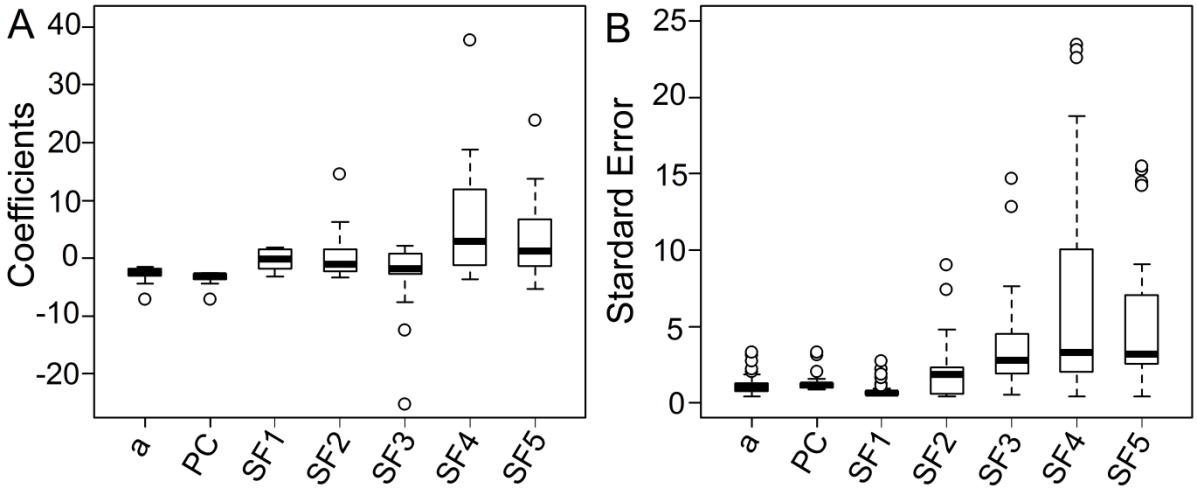
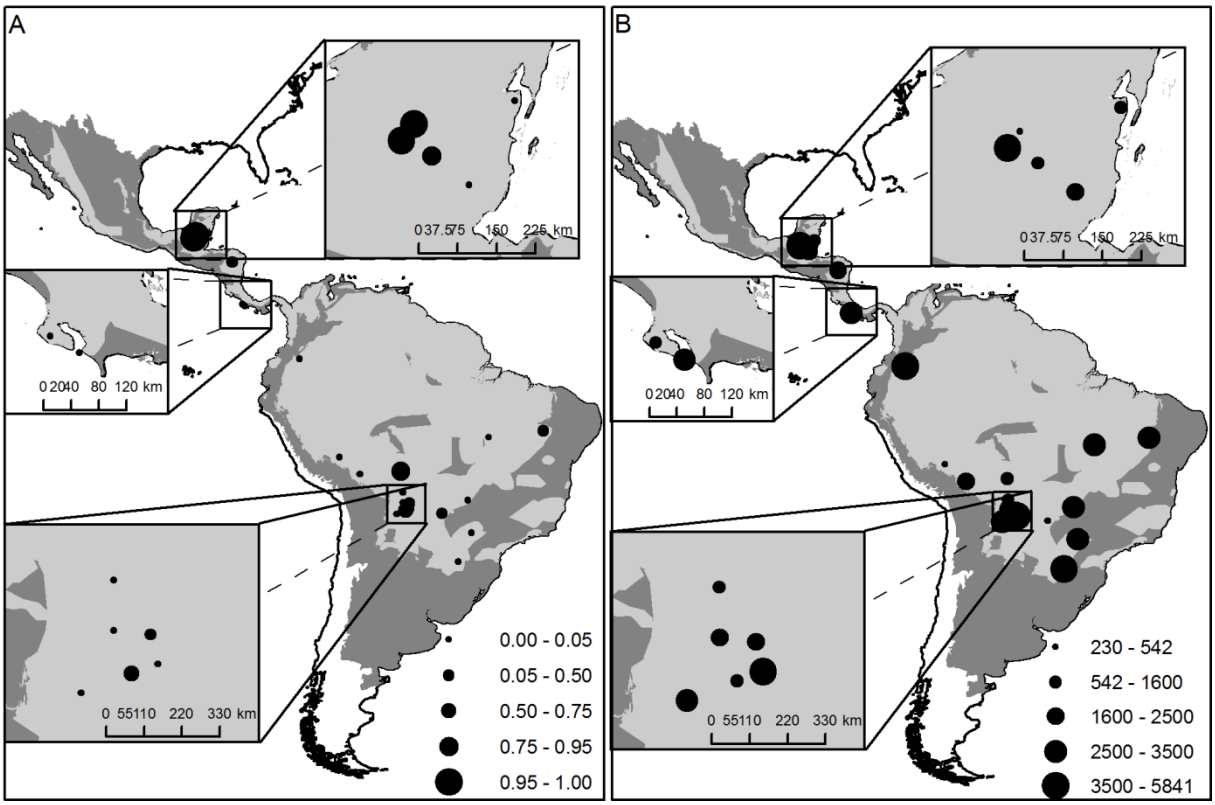



542

543 Figure 1. Variation in coefficients (A) and standard error (B) of the explanatory variables
544 employed to describe jaguar persistence probability: a = coefficient of non-linear regression;
545 PC = first principal component condensing landscape configuration; SF (1-5) = spatial filters
546 capturing differing spatial structures of selected landscapes.




547

548 Figure 2. Maps of the jaguar populations used in our study according to (A) the area

549 requirement (in $km^2$) needed to maintain viable populations (also called the habitat loss

550 critical threshold) and (B) their persistence probabilities in 200 years based on actual

551 landscape configurations. Dark gray indicates original jaguar distribution range (IUCN, 2013)

552 and light gray the current distribution (Zeller, 2007).

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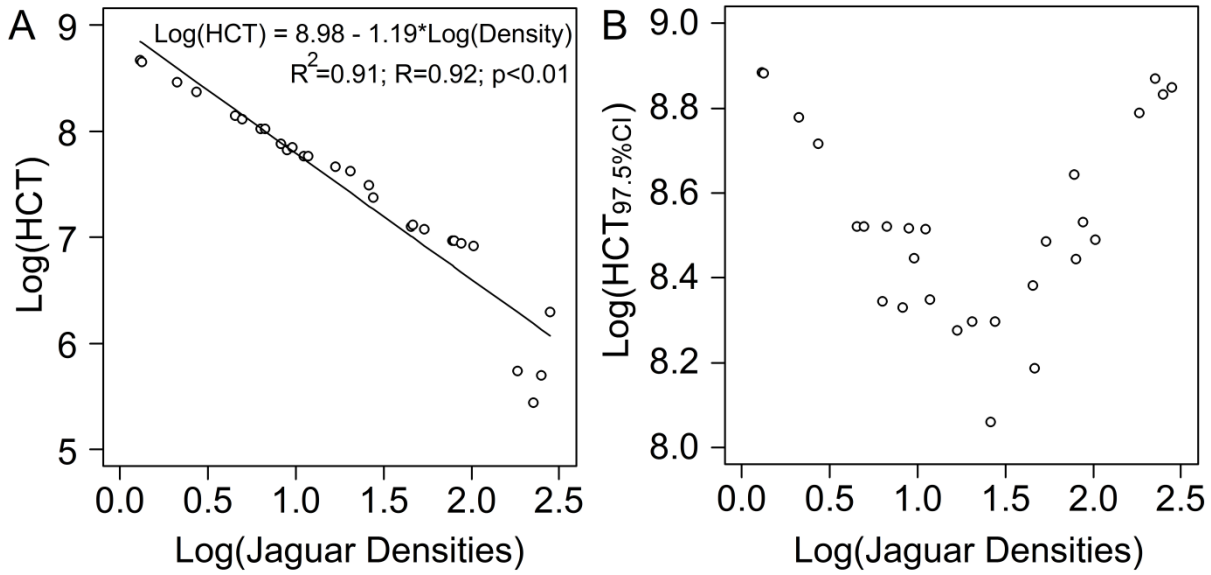



554

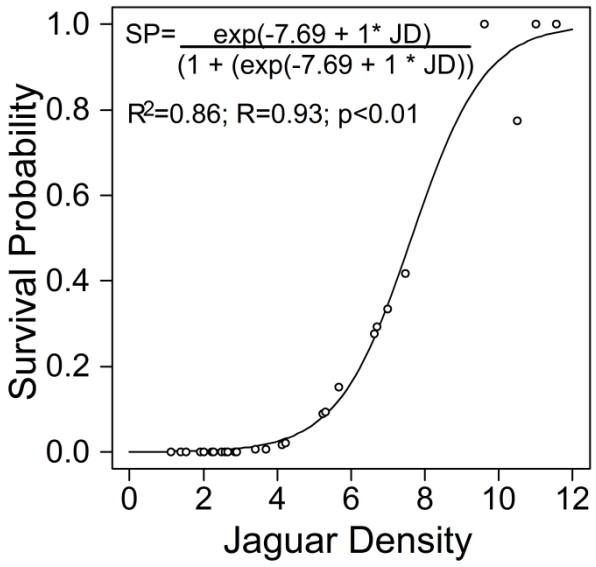
555 Figure 3. Relationship between jaguar density and the habitat loss critical threshold (HCT).

556 (A) Habitat critical threshold estimated to maintain a jaguar population with a high

557 persistence probability. (B) Habitat critical threshold with a 97.5% confidence interval (97.5%

558 CI). The log transformed HCT ranged from 5.3 to 8.9, which is equivalent to a range of 230 to

559 5,841 $km^2$.




560

561 Figure 4. Persistence probability (SP) of metapopulations relative to jaguar density (JD) in

562 landscapes composed of two patches, each of 5,000 km$^2$.

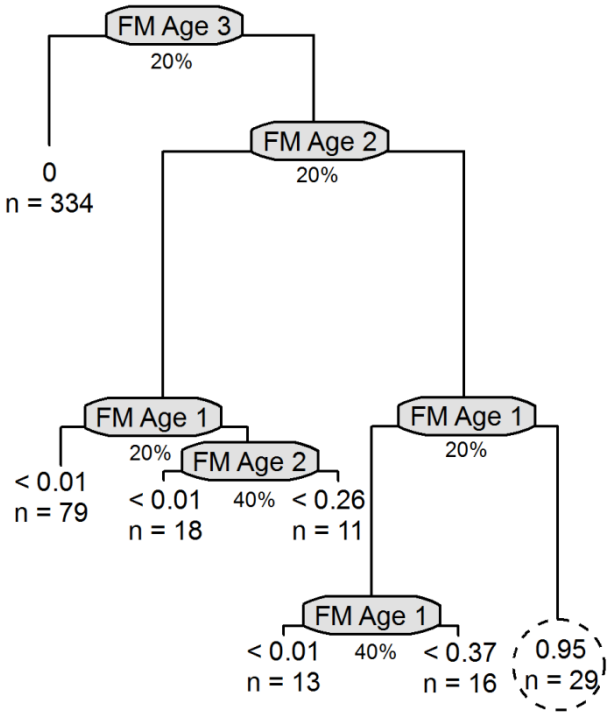
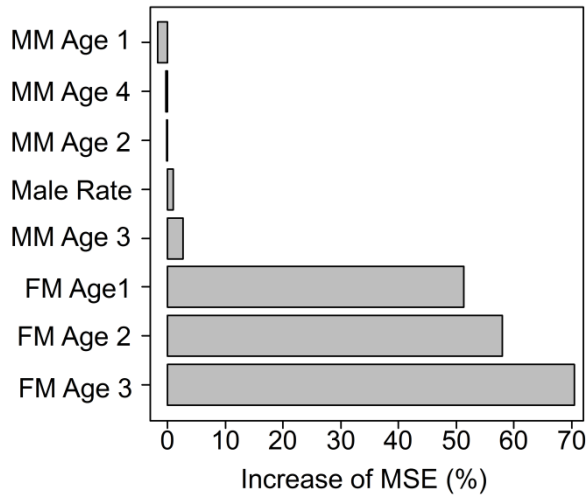



Figure 5. Illustration of the regression tree and the relationships between parameters used to estimate jaguar persistence probability. The significant variables to the regression (gray box) divided the simulated populations into two groups according a value of the variable (percentile bellow gray box is the threshold to division). Populations with values lower or equal than the threshold to division are represented in the left size variable and populations with higher values are in the right size. The final node indicates the probability values along with the number of observations ("n"). FM is female mortality. There is only one pathway (delimited by the circle) that leads to viable populations (high persistence probability).




572

573 Figure 6. Sensitivity of jaguar persistence probability estimates for each variable in the global

574 sensitivity analysis (MM is male mortality and FM female mortality). Mean standard error

575 (MSE) was evaluated by random forest.

576 Table 1. Biological and statistical parameters used in the jaguar population viability analysis.

577 EV - environmental variation; SD - standard deviation.

| Parameter | Value |
|---|---|
| Number of interactions | 1000 |
| Number of years | 200 |
| Extinction | Only 1 sex remains |
| Inbreeding | Yes (Default) |
| EV concordance in persistence and reproduction | Yes (Default) |
| Reproductive system | Polygynous |
| Age of first offspring for females | 3 |
| Age of first offspring for males | 4 |
| Maximum age of reproduction | 10 |
| Maximum number of progeny per year | 4 |
| Sex ratio at birth (% males) | 50 |
| Alle parameter, A | 0.5 |
| Steepness parameter, B | 2 |
| % adult females breeding | $(P0((P0-PK)*((N/K)^2)))*(N/(A+K))$ |
| EV in % breeding | 12.5 |
| EV in % breeding | Specific |
| Adult females producing | |
| 1 young | 5% |
| 2 young | 40% |
| 3 young | 30% |
| 4 young | 25% |

| Parameter | Value |
|---|---|
| Mortality rates in females | |
| Age 0-1 | 34 ± 10 |
| Age 1-2 | 17 ± 8 |
| Age 2-3 (Subadult) | 19 ± 5 |
| Age 3-4 (Adult) | 20 ± 5 |
| Mortality rates in males | |
| Age 0-1 | 34 ± 10 |
| Age 1-2 | 17 ± 8 |
| Age 2-3 (Subadult) | 35 ± 5 |
| Age 3-4 (Subadult) | 30 ± 5 |
| Age 4-5 (Adult) | 30 ± 5 |
| Males in breeding pool | 90% |
| Age distribution | Stable |
| SD carrying capacity | 5% of N(0) |
| Migration rate | 20% |
| Dispersers surviving | 90% |

578

Table 2. Fragmentation metrics used in this study. Abbreviations used in the fragmentation metrics formulae: N - patch number (unit); $a_{ij}$- area of ij patch ($m^2$); A - total area in the landscape ($m^2$); max $a_{ij}$- patch with the largest area ($m^2$); $p_{ij}$- perimeter of patch ij (unit of cells); min $p_{ij}$ - minimum perimeter if patch was maximally aggregated (unit of cells); Z - total number of cells in the landscape.

| Metric | Formula |
|---|---|
| Proportion of landscape with natural vegetation | $\frac{\sum_{j=1}^{N} a_{ij}}{A} \cdot 100$ |
| Largest patch index | $\frac{\max(a_{ij})}{A} \cdot 100$ |
| Landscape shape index | $\frac{p_{ij}}{\min p_{ij}}$ |
| Patch number | $N$ |
| Cohesion | $\left[1 - \frac{\sum_{j=1}^{N} p_{ij}}{\sum_{j=1}^{n} p_{ij}\sqrt{a_{ij}}}\right] \cdot \left[1 - \frac{1}{\sqrt{Z}}\right]^{-1} \cdot 100$ |
| Mean size of patch | $\frac{\sum_{j=1}^{N} a_{ij}}{N}$ |
| Standard deviation of patch area | $\sqrt{\frac{\sum_{j=1}^{N}\left[a_{ij} - \left(\frac{\sum_{j=1}^{N} a_{ij}}{N}\right)\right]^2}{N}}$ |

Table 3. Models with AICc values lower than four describing jaguar persistence probability based on landscape configuration and spatial structure (complete list in Supplementary Material B). PC - first principal component condensing landscape configuration; SF (1-5) - spatial filters capturing the different spatial structures of selected landscapes, DF – degree of freedom, and LL - log-likelihood.

| Variables in the model | Δ AICc | AICc Weighted | Residual Standard Error | DF | LL |
|---|---|---|---|---|---|
| PC, SF3 | 0.00 | 0.24 | 0.25 | 25 | 0.71 |
| PC, SF3, SF5 | 1.93 | 0.09 | 0.25 | 24 | 1.24 |
| PC, SF2, SF3 | 2.17 | 0.08 | 0.25 | 24 | 1.12 |
| PC | 2.53 | 0.07 | 0.27 | 26 | -1.93 |
| PC, SF3, SF4 | 2.80 | 0.06 | 0.25 | 24 | 0.80 |
| PC, SF1, SF3 | 2.94 | 0.05 | 0.25 | 24 | 0.73 |
| PC, SF2, SF5 | 3.08 | 0.05 | 0.26 | 24 | 0.66 |
| PC, SF5 | 3.26 | 0.05 | 0.26 | 25 | -0.92 |